
Lesquerella is United with *Physaria* (Brassicaceae)

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ABSTRACT. *Lesquerella* (Brassicaceae) is united with the earlier-published *Physaria* following an unsuccessful attempt to conserve the more speciose *Lesquerella*. Molecular, morphological, distributional, and ecological data strongly support the union of the two genera. Ninety-one names in *Lesquerella*, including 75 at the specific rank, are transferred to *Physaria*. The new names *P. nelsonii* and *P. reediana* are proposed to avoid the creation of later homonyms in *Physaria*.

Key words: Brassicaceae, *Lesquerella*, North America, *Paysonia*, *Physaria*.

The genus *Physaria* (Nuttall ex Torrey & A. Gray) A. Gray was initially described in Torrey and Gray (1838) as a section of the Old World genus *Vesicaria* Adanson and was later raised to the generic rank by Gray (1848). As presently circumscribed (Rollins, 1993), *Physaria* consists of 22 species distributed from North Dakota south into Nebraska, Colorado, and New Mexico, and west through the Mountain and Pacific states, with the range of one species, *P. didymocarpa* (Hooker) A. Gray, extending into southern Alberta, Canada. With the exception of *P. alpestris* Suksdorf, *P. geyeri* (Hooker) A. Gray, and *P. oregona* S. Watson, most of the remaining 19 species occur in Colorado, Utah, or Wyoming. Both *P. didymocarpa* and *P. geyeri* were originally described in *Vesicaria*, but this generic name is illegitimate because it included the type of the earlier published *Alyssoides* Miller. As many as 37 taxa of North American Brassicaceae (see Rollins & Shaw, 1973; Rollins, 1993) were originally described in *Vesicaria*, but the vast majority of those were later transferred to *Lesquerella* S. Watson (Watson, 1888).

Lesquerella was established by Watson (1888) as a North American genus distinguished from the exclusively Mediterranean *Vesicaria* by having edentate versus dentate filaments and veined instead of veinless septa. Watson (1888) and Payson (1922)

recognized 33 and 52 species in *Lesquerella*, respectively. Rollins (1993) recognized 83 species of *Lesquerella* in North America, with the range of one, *L. arctica* (Wormskjöld ex Hornemann) S. Watson, extending into Greenland, northern Canada, Alaska, and Arctic Russia (Rollins & Shaw, 1973; Tolmachev, 1975). Five additional North American species were subsequently described (Rollins, 1995; Rollins et al., 1996; Anderson et al., 1997; O'Kane, 1999). Although Boelcke and Romanczuk (1984) recognized a single species from Argentina (and Bolivia), we believe that an additional four or five new species grow in southern South America. The taxonomy of the South American species of *Physaria* will be published at a later date.

In his *Cruciferae of Continental North America*, Rollins (1993) separated *Physaria* from *Lesquerella* primarily on the basis of *Physaria* having strongly didymous fruits with deep sinuses between the valves distally (apically), and often proximally (basally) as well, as compared to *Lesquerella*, which has non-didymous fruits with no, or shallow, distal sinuses. Additionally, *Physaria* was said to have siliques compressed perpendicular to the replum while *Lesquerella* has fruits compressed parallel to the replum or not at all, a dichotomy that is violated in several taxa. *Lesquerella* and *Physaria* are indistinguishable in basically every other morphological aspect, including leaf morphology, trichome type, inflorescence, flower color, fruiting pedicels, and all aspects of seed-coat sculpture and embryo type. This remarkable similarity was expressed by Rollins (1939: 393), who stated, "The natural relationship between *Physaria* and *Lesquerella* is very marked. These two genera have almost exactly the same floral pattern, habit of growth, and trichome morphology. The siliques too are very similar." With the exception of the South American species and the auriculate-leaved species of *Lesquerella* of the southeastern United States, *Physaria* and *Lesquerella* have a coherent geographical distribution.

The geographic range of *Physaria* falls perfectly within that of *Lesquerella*, which is widespread in the dry western United States and northern Mexico. Furthermore, species of both genera primarily occupy arid substrates supporting sparse vegetation. In some cases, a species of *Physaria* or *Lesquerella* may be the only, or one of a very few, species on a site. Many of the species of these genera are rare, and some are included on the United States list of Endangered and Threatened Species.

The degree of development of the apical and/or basal sinuses among species of *Lesquerella* and *Physaria*, and therefore, whether the fruit becomes didymous or not, is a quantitative character that shows continuity from one end of the spectrum to the other. All workers who studied these two genera were unable to draw a natural line between them. For example, Payson (1922: 221), who critically examined the boundaries between these genera, stated, "So striking, indeed, is this similarity that one is a little perplexed at times to know to which genus a given plant should be referred," and "The bridge connecting the two genera is nearly complete." Furthermore, Rollins (1950: 46) indicated that "The evidence now assembled shows a continuous morphological gradation from the genus *Physaria* into *Lesquerella*. This evidence has been accumulating almost since the time Watson (1888) founded *Lesquerella* as a genus distinct from *Vesicaria*," and "Thus the assumed gap between these genera has been completely closed insofar as the morphology of the various entities involved is concerned." Maguire (1942) and Maguire and Holmgren (1951) also expressed their dissatisfaction about the delimitation of both genera, as did Mulligan (1968), who critically examined borderline species and transferred three species from *Physaria* to *Lesquerella*.

All the authors above have clearly indicated that there are no adequate morphological grounds to support the maintenance of *Lesquerella* and *Physaria* as separate genera. Although Rollins and Rüdénberg (1971) hinted that chromosome size of *Physaria* might be different from that of *Lesquerella*, subsequent studies (Rollins & Rüdénberg, 1977, 1979) did not support that assumption. Two main reasons explain why both genera have been maintained by previous authors. First, authors have followed tradition and ignored the lack of convincing morphologies separating the two genera. Second, authors simply avoided the transfer of the numerous species of *Lesquerella* to the much smaller and earlier-published *Physaria*. Such arguments were presented by Rollins and Shaw (1973: 5) who, paradoxically, stated that "Nothing is gained for the classification of either *Lesquerella* or *Physaria* by

abandoning the *traditional line of demarcation* between them" (italics, ours) and "We interpret the evidence . . . as once again emphasizing the step-by-step continuity between these genera. The line to be drawn between the genera is an arbitrary one, and for this reason we think it should remain as it has been accepted for many years." Such reasoning does not justify the maintenance of both genera, especially when molecular data are taken into consideration.

One of the present authors (SLO) has been working on the phylogeny of the *Physaria*–*Lesquerella* complex for the past four years using molecular tools. The molecular data clearly show that *Physaria* is nested within and evolved more than once from *Lesquerella*. These results are primarily from DNA sequences of the internal transcribed spacer (ITS; Baldwin et al., 1995) of nuclear ribosomal DNA. Less complete data from length variation of the region between microsatellite loci, called inter-simple sequence repeat regions (ISSR; Zietkiewicz et al., 1994), support these conclusions. Regardless of the number of derivations of *Physaria* from *Lesquerella*, the former genus is polyphyletic and the latter is definitely paraphyletic. Molecular data (O'Kane, unpublished) do not support any regrouping of the species that would allow the recognition of both *Physaria* and *Lesquerella*. The two genera can no longer be maintained on molecular, morphological, cytological, biogeographic, and ecological grounds. *Lesquerella* and *Physaria* (hereafter combined as *Physaria*), together with *Dimorphocarpa* Rollins, *Dithyrea* Harvey, *Lyrocarpa* Hooker & Harvey, *Nerisyrenia* Greene, and *Synthlipsis* A. Gray, are characterized by having 4–10-colpate pollen grains (Rollins, 1979; Rollins & Shaw, 1973; Rollins & Banerjee, 1979), a synapomorphy that distinguishes these genera from the rest of the family, which have tricolpate pollen grains. Molecular data (O'Kane, unpublished) also support the monophyly of this *Physaria* alliance.

In order to avoid the massive transfer of species from the later-published *Lesquerella* to the earlier-published *Physaria*, O'Kane et al. (1999) proposed to conserve *Lesquerella* with a conserved type. By conserving *Lesquerella*, one avoids the transfer of 91 names from *Lesquerella* to *Physaria*. Only 20 species names in *Physaria* would have been transferred to *Lesquerella*. It is rather unfortunate that the Committee for Spermatophyta (Brummitt, 2000) did not take the above overwhelming arguments into consideration when it decided by a vote of ten to five to reject the proposal because (p. 804) "The feeling of a majority of the Committee is that in the present case the name *Physaria* is already well

known and the advantages of conservation are not sufficient to justify over-ruling the principle of priority." We disagree with this reasoning and are forced to take one of two actions. First, maintain both genera, which would mean that a paraphyletic *Lesquerella* and polyphyletic *Physaria* should be recognized. However, this solution would mean that taxonomy should be practiced without regard to evolutionary or phylogenetic considerations, a course of action unacceptable to us. Therefore, we are left with the second option, to unite the two genera. We certainly would have preferred to do so by the conservation of *Lesquerella*. The extensive transfer of species from *Lesquerella* to *Physaria* is here made so that names are available for floristic works in progress, including the *Flora of North America*, the *Flora of the San Juan Basin*, and the *Arizona Flora*.

The eight auriculate-leaved species previously included in *Lesquerella* are excluded from this treatment and will be transferred to a new genus in a separate publication (see this issue of *Novon*). The South American *Physaria* (previously *Lesquerella*) will also be treated in another publication. Nomenclatural adjustments made here, then, are only for North American species. Therefore, as presently circumscribed, the genus *Physaria* in North America consists of 98 species, including 22 maintained in that genus by Rollins (1993), 75 transferred herein from *Lesquerella* to *Physaria*, and 2, *P. cordiformis* Rollins and *P. montana* (A. Gray) E. L. Greene, originally described in or transferred to *Physaria*, respectively.

Following the new combinations and new names given below, the basionym and the synonym in *Lesquerella* (when applicable) are cited. The complete synonymy is given in Rollins and Shaw (1973) and Rollins (1993).

Physaria angustifolia (Nuttall ex Torrey & A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria angustifolia* Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 101. 1838. TYPE: U.S.A. Oklahoma: Choctaw Co., Red River, *Thomas Nuttall s.n.* (lectotype, designated by Rollins (1956), BM; isoelectotype, K).

Physaria arctica (Wormskjöld ex Hornemann) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Alyssum arcticum* Wormskjöld ex Hornemann, Fl. Dan. 9, Fasc. 26, 5, t. 1520. 1818. *Lesquerella arctica* (Wormskjöld ex Hornemann) S. Watson, Proc. Amer. Acad. Arts. 23: 254. 1888. TYPE: Greenland. Omenak, *C. L. Giesecke s.n.* (holotype, C).

Physaria arenosa (Richardson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria arenosa* Richardson, in Franklin, App. Narr. Journey Polar Sea 743. 1823. *Lesquerella arenosa* (Richardson) Rydberg, Bull. Torrey Bot. Club 29: 236. 1902. TYPE: Canada. Plains of Saskatchewan, *John Richardson 252* (holotype, K; isotype, GH).

Physaria arenosa* subsp. *argillosa (Rollins & Shaw) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella arenosa* var. *argillosa* Rollins & Shaw, Genus *Lesquerella* in N. Amer. 178. 1973. TYPE: U.S.A. South Dakota: Pennington Co., along bed of creek near Piedmont, *E. J. Palmer 37016* (holotype, GH).

Physaria argentea (Schauer) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria argentea* Schauer, Linnaea 20: 720. 1847. *Lesquerella argentea* (Schauer) S. Watson, Proc. Amer. Acad. Arts 23: 252. 1888, non *L. argentea* (Pursh) MacMillan, Metasp. Minnesota Valley 263. 1892. TYPE: Mexico. Without locality, *Aschenborn 278* (holotype, B).

Physaria argyraea (A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria argyraea* A. Gray, Bost. J. Nat. Hist. 6: 146. 1850. *Lesquerella argyraea* (A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 254. 1888. TYPE: U.S.A. Texas: Calhoun Co., banks of Green Lake, near Matagorda Bay, *F. Lindheimer 329* (lectotype, designated by Rollins & Shaw (1973), GH; isoelectotype, MO).

Physaria argyraea* subsp. *diffusa (Rollins) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella diffusa* Rollins, J. Arnold Arbor. 21: 395. 1940. TYPE: Mexico. Nuevo León: Galeana, 5400 ft., *Chase 7750* (holotype, GH; isotypes, ARIZ, F).

Rollins (1993) reduced *Lesquerella diffusa* to a variety of *L. argyraea*, a position that we support at the subspecific rank under *Physaria*.

Physaria arizonica (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella arizonica* S. Watson, Proc. Amer. Acad. Arts 23: 254. 1888. TYPE: U.S.A. Arizona: Yavapai Co., Juniper Mesa, near Prescott, Apr. 1876, *Edward Palmer 16* (lectotype, designated by Rollins & Shaw (1973), GH; isoelectotypes, F, M, MO, NY, US).

- Physaria aurea** (Wooton) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella aurea* Wooton, Bull. Torrey Bot. Club 25: 260. 1898. TYPE: U.S.A. New Mexico: S fork of Tularosa Creek, 3 mi. E of Mescalero Agency, White Mts., 30 July 1897, *Elmer O. Wooton 245* (holotype, US; isotypes, B, K, MO, NDG, NMC, NY, RM, UC).
- Physaria berlandieri** (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella berlandieri* S. Watson, Proc. Amer. Acad. Arts 23: 252. 1888. TYPE: Mexico. Tamaulipas: near Matamoros, *Berlandier 884* (lectotype, designated by Payson (1922), GH).
- Physaria calcicola** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella calcicola* Rollins, Amer. J. Bot. 26: 419. 1939. TYPE: U.S.A. Colorado: Las Animas Co., 3 mi. E of San Francisco Creek, 8 mi. NW of Trinchera, 13 July 1937, *Reed C. Rollins 1861* (holotype, GH; isotypes, MO, NY, OKL, UC, US, UTC).
- Physaria calderi** (G. Mulligan & A. Porsild) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella calderi* G. Mulligan & A. Porsild, Canad. J. Bot. 47: 215. 1969. TYPE: Canada. Yukon Territory: Cathedral Rocks, Ogilvie Mts., 66°2'N, 138°44'W, 3500 ft., 29 June 1960, *J. A. Calder & J. M. Gillett 26016* (holotype, DAO; isotypes, CAN, GH).
- Physaria carinata** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella carinata* Rollins, Contr. Gray Herb. 171: 42. 1950. TYPE: U.S.A. Idaho: Lemhi Co., Birch Creek, Range 29 East-Township 11 North, 3 July 1941, *Ray J. Davis 3801* (holotype, GH).
- Lesquerella carinata* var. *languida* Rollins, Cruciferae of Continental N. Amer. 611. 1993. Syn. nov. TYPE: U.S.A. Montana: Granite Co., Rattler Gulch, ca. 4 mi. NW of Drummond, T11N, R13W, Sec. 10, SW ¼, Sec. 9, SE ¼, 4050 ft., 12 June 1990, *Lisa Ann Schassberger 364 & Diane Pavsek* (holotype, GH).
- Physaria cinerea** (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella cinerea* S. Watson, Proc. Amer. Acad. Arts 23: 255. 1888. TYPE: U.S.A. Arizona: without locality, 1869, *Edward Palmer s.n.* (holotype, US).
- Physaria congesta** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella congesta* Rollins, Contr. Gray Herb. 214: 8. 1984. TYPE: U.S.A. Colorado: Rio Blanco Co., Green River Formation, North Dudley Gulch, ca. 3/4 mi. NE of junction of Dudley Gulch and Piceance Creek, T2S, R97W, Sec. 4, 20 June 1893, *Reed C. & Kathryn W. Rollins 8394 with Scott Peterson, Aileen G. Roads, Karen Wiley-Eberle & Dieter Wilken* (holotype, GH; isotype, MO).
- Physaria densiflora** (A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria densiflora* A. Gray, Bost. J. Nat. Hist. 6: 145. 1850. *Lesquerella densiflora* (A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 251. 1888. TYPE: U.S.A. Texas: Gillespie Co., Fredericksburg, May 1847, *F. Lindheimer 577* (lectotype, designated by Rollins & Shaw (1973), GH; isotype, M).
- Physaria douglasii** (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella douglasii* S. Watson, Proc. Amer. Acad. Arts 23: 255. 1888. TYPE: U.S.A. Columbia Valley, 1860, *Lyall s.n.* (lectotype, designated by Rollins & E. Shaw (1973), GH).
- Physaria douglasii** subsp. **tuplashensis** (Rollins, Beck & Caplow) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella tuplashensis* Rollins, Beck & Caplow, Rhodora 97: 203. 1996. TYPE: U.S.A. Washington: Franklin Co., White Bluffs, T13N, R27E, S11, W1/2, above Columbia River, 20 July 1994, *Kathryn A. Beck & Florence E. Caplow 94001* (holotype, GH; isotype, WTU).
- Rollins et al. (1996) recognized that both *Lesquerella tuplashensis* and *L. douglasii* are quite similar morphologically, and that they differ primarily by the former having a raised instead of an appressed radiate portion of the trichomes. In our opinion, these differences do not justify the recognition of two distinct species.
- Physaria engelmannii** (A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria engelmannii* A. Gray, Gen. Amer. Bor.-Orient. Ill. 1: 162, pl. 70. 1848. *Lesquerella engelmannii* (A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 254. 1888. TYPE: U.S.A. Texas: shores of Guadalupe, New Braunfels, May 1846, *F. Lindheimer 325* (holotype, GH; isotypes, B, GH, K, MO).

- Physaria fendleri*** (A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria fendleri* A. Gray, Mem. Amer. Acad. Arts 4: 9. 1849. *Lesquerella fendleri* (A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 254. 1888. TYPE: U.S.A. New Mexico: around Santa Fe, 2 Apr. 1847, A. Fendler 40 (holotype, MO).
- Physaria filiformis*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella filiformis* Rollins, Rhodora 58: 201. 1956. TYPE: U.S.A. Missouri: Dade Co., Turnback, 5 May 1929, Palmer 35604 (holotype, GH; isotypes, F, MO, NY, US).
- Physaria fremontii*** (Rollins & E. Shaw) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella fremontii* Rollins & E. Shaw, Genus *Lesquerella* in N. Amer. 228. 1973. TYPE: U.S.A. Wyoming: Fremont Co., Wind River Mts., 5 mi. E of Atlantic City, 8200 ft., Harry D. Ripley & Rupert C. Barneby 8931 (holotype, CAS; isotypes, NY, US).
- Physaria garrettii*** (Payson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella garrettii* Payson, Ann. Missouri Bot. Gard. 8: 213. 1922. TYPE: U.S.A. Utah: Salt Lake Co., Big Cottonwood Canyon, 9700 ft., 28 June 1905, Albert O. Garrett 1344 (holotype, MO; isotypes, GH, RM).
- Physaria globosa*** (Desvaux) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria globosa* Desvaux, J. Bot. Agric. 3: 184. 1815. *Lesquerella globosa* (Desvaux) S. Watson, Proc. Amer. Acad. Arts 23: 252. 1888. TYPE: U.S.A. "Cet-te plante croit dans les lieux arides de l'Amérique septentrionale," without collector name (holotype, P).
- Physaria gooddingii*** (Rollins & E. Shaw) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella gooddingii* Rollins & E. Shaw, Genus *Lesquerella* in N. Amer. 164. 1973. TYPE: U.S.A. New Mexico: Catron Co., along Tularosa Creek, 5 mi. SW of Apache Creek, 4 Sep. 1956, Rupert C. Barneby 12923 (holotype, CAS).
- Physaria goodrichii*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella goodrichii* Rollins, J. Arnold Arbor. 64: 503. 1983. TYPE: U.S.A. Utah: Millard Co., Desert Experimental Range, Tunnel Springs Mts., 21 mi. SE of Garrison, T24S, R17W, S9, 8000 ft., 16 June 1982, Sherel Goodrich 16951 (holotype, GH; isotypes, BRY, NY, UTC).
- Physaria gordonii*** (A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria gordonii* [as *gordoni*] A. Gray, Bost. J. Nat. Hist. 6: 149. 1850. *Lesquerella gordonii* S. Watson, Proc. Amer. Acad. Arts 23: 253. 1888. TYPE: U.S.A. New Mexico: Canadian River, Raton Mts., Apr. 1848, A. Gordon 4 (holotype, GH; isotype, MO).
- Physaria gordonii* subsp. *densifolia*** (Rollins) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella gordonii* var. *densifolia* Rollins, Cruciferae Continental N. Amer. 621. 1993. TYPE: U.S.A. New Mexico: Lincoln Co., ca. 2 mi. N of Lincoln, off US Hwy. 380, 13 Apr. 1990, Reed C. & Kathryn W. Rollins 9046 (holotype, GH).
- Physaria gracilis*** (Hooker) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria gracilis* Hooker, Curtis's Bot. Mag., n.s. 10: t. 3533. 1836. *Lesquerella gracilis* (Hooker) S. Watson, Proc. Amer. Acad. Arts 23: 253. 1888. TYPE: U.S.A. Texas: San Felipe, Drummond III 13 (holotype, K; isotype, GH).
- Physaria gracilis* subsp. *nuttallii*** (Torrey & A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria nuttallii* Torrey & A. Gray, Fl. N. Amer. 1: 101. 1838. *Lesquerella gracilis* subsp. *nuttallii* (Torrey & A. Gray) Rollins & E. Shaw, Genus *Lesquerella* in N. Amer. 53. 1973. TYPE: U.S.A. "Prairies of the Red River," Melines C. Leavenworth s.n. (lectotype, designated by Rollins & Shaw (1973), GH).
- Physaria hemiphsaria*** (Maguire) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella hemiphsaria* Maguire, Amer. Midl. Naturalist 27: 466. 1942. TYPE: U.S.A. Utah: Sanpete Co., S side Middle Forks Park, Wasatch Plateau, 10,800 ft., 10 Aug. 1940, Bassett Maguire 20053 (holotype, UTC; isotype, DS).
- Physaria hemiphsaria* subsp. *lucens*** (Welsh & Reveal) O'Kane & Al-Shehbaz, comb. et stat. nov. *Lesquerella hemiphsaria* var. *lucens* Welsh & Reveal, Great Basin Naturalist 37: 338. 1977. TYPE: U.S.A. Utah: Carbon Co., 7 mi. NE of Sunnyside, Range Creek Canyon, 23 June 1977, Stanley L. Welsh & K. Taylor 15139 (holotype, BRY).

Physaria hitchcockii (Munz) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella hitchcockii* Munz, Bull. Torrey Bot. Club 56: 163. 1929. TYPE: U.S.A. Nevada: Clark Co., Charleston Mts., 1 Sep. 1927, 10,500 ft., *E. C. Jaeger* & *C. Leo Hitchcock s.n.* (holotype, POM).

Physaria hitchcockii subsp. **rubicundula** (Rollins) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella rubicundula* Rollins, Contr. Dudley Herb. 3: 178. 1941. TYPE: U.S.A. Utah: Garfield Co., Red Canyon, ca. 12 mi. E of Bryce Junction, Sevier Forest (now Powell National Forest), 6 July 1912, *Willard W. Eggleston 8198* (holotype, NA).

The main differences given by Rollins (1993) to separate *Lesquerella hitchcockii* from *L. rubicundula* (e.g., racemes exserted vs. embedded among the basal leaves, smooth vs. tuberculate trichomes, and leaves attenuate at base vs. petiolate, respectively) are variable and often not correlated. While *L. rubicundula* does have some smooth trichomes, most trichomes are tuberculate and indistinguishable from those in *L. hitchcockii*. The two species are also indistinguishable molecularly (O'Kane, unpublished) and cytologically (Windham & O'Kane, unpublished). Maguire and Holmgren (1951) and Barneby (1966) treated *L. rubicundula* as a subspecies of *L. hitchcockii*, a position we agree with. Rollins also reduced *L. tumulosa* to synonymy of *L. rubicundula*, a relationship that is also not substantiated on molecular and cytological grounds.

Physaria humilis (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella humilis* Rollins, Contr. Gray Herb. 214: 9. 1984. TYPE: U.S.A. Montana: Ravalli Co., near summit of St. Mary's Peak, Bitterroot Range, 17 July 1983, *Reed C. & Kathryn W. Rollins 83300*, with *Klaus H. Lackschewitz*, *Peter Lesica* & *Aileen G. Roads* (holotype, GH).

Physaria inflata (Rollins & E. Shaw) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella inflata* Rollins & E. Shaw, Genus *Lesquerella* in N. Amer. 150. 1973. TYPE: Mexico. Nuevo León: between Saltillo and Monterrey, along Rte. 40, km 351, ca. 200 yards E of weighing station, 14 Feb. 1969, *Spetzman 1212* (holotype, GH).

Physaria intermedia (S. Watson) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella alpina* (Nuttall ex Torrey & A. Gray) S. Watson var. *intermedia* S. Watson, Proc. Amer. Acad. Arts 23: 251. 1888. TYPE: U.S.A. New Mexico: W of Sante Fe, *A. Fendler 38* (lectotype, designated by Rollins & Shaw (1973), GH).

Physaria johnstonii (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella johnstonii* Rollins, Contr. Dudley Herb. 3: 179. 1941. TYPE: Mexico. Coahuila: Sierra del Piño, ca. 10 mi. N of camp at La Noria, *Ivan M. Johnston & Cornelius H. Muller 556* (holotype, GH).

Physaria kingii (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria kingii* S. Watson, Proc. Amer. Acad. Arts 20: 353. 1885. *Lesquerella kingii* (S. Watson) S. Watson, Proc. Amer. Acad. Arts 23: 251. 1888. TYPE: U.S.A. Nevada: Pershing Co., West Humboldt Mts., June 1868, *Sereno Watson 82* (lectotype, designated by Payson (1922), GH; isoelectotype, NY).

The following subspecies of *Physaria kingii* were variously recognized by Rollins (1993) and Rollins and Shaw (1973) as varieties and/or subspecies under *Lesquerella kingii*.

Physaria kingii subsp. **bernardina** (Munz) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella bernardina* Munz, Bull. S. Calif. Acad. Sci. 31: 62. 1932. TYPE: U.S.A. California: San Bernardino Co., N side of Bear Lake, E end of Bear Valley, San Bernardino Mts., 16 May 1924, *Frank W. Peirson 4600* (holotype, POM; isotypes, GH, JEPS, RM, RSA).

Physaria kingii subsp. **cobrensis** (Rollins & E. Shaw) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella kingii* subsp. *kingii* var. *cobrensis* Rollins & E. Shaw, Genus *Lesquerella* in N. Amer. 255. 1973. TYPE: U.S.A. Nevada: Elko Co., 30 mi. E of Wells on Cobre old Hwy. paralleling Southern Pacific Railroad, *Percy Train 3665* (holotype, GH; isotypes, NY, UC).

- Physaria kingii* subsp. *diversifolia*** (E. L. Greene) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella diversifolia* E. L. Greene, Pittonia 4: 309. 1901. TYPE: U.S.A. Oregon: Wallowa Co., Wallowa Mts., 7000 ft., 6 Aug. 1899, *Cusick 2304* (holotype, NDG; isotypes, F, GH, MO, UC, US, WS).
- Physaria kingii* subsp. *latifolia*** (A. Nelson) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella latifolia* A. Nelson, Bot. Gaz. 42: 49. 1906. TYPE: U.S.A. Nevada: Lincoln Co., Karshaw, Meadow Valley Wash, 26 Apr. 1902, *Leslie N. Goodding 625* (holotype, RM; isotypes, GH, MO, US).
- Physaria klausii*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella klausii* Rollins, Contr. Gray Herb. 214: 10. 1984. TYPE: U.S.A. Montana: Lewis and Clark Co., W side above Hwy. 200 at Rogers Pass, 5800 ft., 25 July 1982, *Klaus H. Lackschewitz & David Ramsden 10112* (holotype, MONTU).
- Physaria lata*** (Wooton & Standley) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella lata* Wooton & Standley, Contr. U.S. Natl. Herb. 16: 126. 1913. TYPE: U.S.A. New Mexico: Lincoln Co., near Lincoln National Forest, 1903, *Fred G. Plummer s.n.* (holotype, US).
- Physaria lesicii*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella lesicii* Rollins, Novon 5: 71. 1995. TYPE: U.S.A. Montana: Carbon Co., ridge W of Layout Creek, ½ mi. S of Mystery Cave, Pryor Mts., 7500 ft., T85, R28E, S21, SW ¼, 20 June 1992, *Peter Lesica 5707 & Rob DeVelica* (holotype, GH).
- Physaria lindheimeri*** (A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria lindheimeri* A. Gray, Bost. J. Nat. Hist. 6: 145. 1850. *Lesquerella lindheimeri* (A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 253. 1888. TYPE: U.S.A. Texas: lower Guadeloupe, E of Victoria, Feb. 1845, *F. Lindheimer 327* (holotype, GH; isotypes, B, GH, K, MO).
- Physaria ludoviciana*** (Nuttall) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Alyssum ludovicianum* Nuttall, Gen. N. Amer. Pl. 2: 63. 1818; based on *Myagrum argenteum* Pursh, Fl. Amer. Septen. 2: 434. 1814, not *A. argenteum* Vitmann, Summa 4: 30. 1790. *Lesquerella ludoviciana* (Nuttall) S. Watson, Proc. Amer. Acad. Arts 23: 252. 1888. TYPE: U.S.A. Banks of the Missouri, *Thomas Nuttall s.n.* (lectotype, designated by Rollins & Shaw (1973), PH; isolectotype, BM).
- Physaria macrocarpa*** (A. Nelson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella macrocarpa* A. Nelson, Bot. Gaz. 34: 366. 1902. TYPE: U.S.A. Wyoming: Sweetwater Co., Bush Ranch, 10 June 1900, *Aven Nelson 7081* (holotype, RM; isotypes, B, COLO, GH, K, MO, NY, US).
- Physaria mcvaughiana*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella mcvaughiana* Rollins, Contr. Gray Herb. 171: 44. 1950. TYPE: U.S.A. Texas: Brewster Co., E of Mt. Ord, Sierra del Norte, ca. 10 mi. SE of Alpine, 7 Apr. 1947, *Rogers McVaugh 7862* (holotype, GH; isotype, A).
- Physaria mexicana*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella mexicana* Rollins, Bol. Soc. Bot. México 23: 45. 1958. TYPE: Mexico. Coahuila: 43 mi. S of Monclova, 14 Aug. 1948, *Kenoyer & Crum 2625* (holotype, GH).
- Physaria mirandiana*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella mirandiana* Rollins, Bol. Soc. Bot. México 23: 43. 1958. TYPE: Mexico. Nuevo León: Cañon de los Capulines, above San Enrique, Hacienda San José de Raíces, Municipio de Derumbadero, 6 Aug. 1935, *C. H. Muller 2412* (holotype, GH; isotypes, F, MO).
- Physaria multiceps*** (Maguire) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella multiceps* Maguire, Amer. Midl. Naturalist 27: 465. 1942. TYPE: U.S.A. Utah: Cache Co., vicinity of Tony Grove Lake, Bear River Range, 8300 ft., 4 Aug. 1838, *Bassett Maguire 16030* (holotype, UTC; isotypes, DS, GH, RM, UC).
- Physaria navajoensis*** (O'Kane) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella navajoensis* O'Kane, Madroño 46: 88. 1999. TYPE: U.S.A. New Mexico: McKinley Co., ca. 2 air mi. NE of Thoreau on bench below and SE of Mt. Powell, 35°26'8"N, 108°12'26"W, 7600 ft. (2316 m), 23 May 1998, *Steve L. O'Kane, Jr. 4232 & Daniela Roth* (holotype, MO; isotypes, BRY, COLO, GH, ISTC, NMC, NY, RM, UNM).

Physaria nelsonii O'Kane & Al-Shehbaz, nom. nov. Replaced name: *Lesquerella condensata* A. Nelson, Bull. Torrey Bot. Club 26: 238. 1899, not *Physaria condensata* Rollins, Rhodora 41: 407. 1939. TYPE: U.S.A. Wyoming: Sweetwater Co., Tipton, *Aven Nelson* 4797 (lectotype, designated by Payson (1922), RM; isoelectotypes, GH, NY).

The species is named in honor of Aven Nelson (24 March 1859–31 March 1952) who described numerous novelties in the Brassicaceae of the Rocky Mountain flora. The transfer of *Lesquerella condensata* to *Physaria* would create a later homonym of *P. condensata* Rollins (Rollins, 1939).

Physaria obdeltata (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella obdeltata* Rollins, Cruciferae Continental N. Amer. 640. 1993. TYPE: U.S.A. Idaho: Bingham Co., near Middle Butte, off road T-4, 3.5 mi. E of U.S. Hwy. 26, 24 June 1986, *Reed C. & Kathryn W. Rollins* 8695 (holotype, GH).

Physaria occidentalis (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria occidentalis* S. Watson, Proc. Amer. Acad. Arts 20: 353. 1885. *Lesquerella occidentalis* (S. Watson) S. Watson, Proc. Amer. Acad. Arts 23: 251. 1888. TYPE: U.S.A. California: Siskiyou Co., Humbug Hills, near Yreka, 30 June 1876, *Edward L. Greene* 902 (lectotype, designated by Hitchcock et al. (1964), GH).

Physaria occidentalis subsp. **cinerascens** (Maguire & A. Holmgren) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella occidentalis* subsp. *diversifolia* (Greene) Maguire & A. Holmgren var. *cinerascens* Maguire & A. Holmgren, Madroño 11: 178. 1951. TYPE: U.S.A. Nevada: White Pine Co., White Pine Mts., NE of Hamilton, *Harry D. Ripley & Rupert C. Barneby* 9295 (holotype, NE; isotypes, UC, UTC).

Physaria ovalifolia (Rydberg) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella ovalifolia* Rydberg, in Britton & A. Brown, Ill. Fl. N. U.S. 2: 137. 1897. TYPE: U.S.A. Nebraska: Kimball Co., hills of upper Lawrence Fork, 11 Aug. 1891, *Per A. Rydberg* 22 (holotype, NY; isotypes, NY, US).

Physaria ovalifolia subsp. **alba** (Goodman) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella ovalifolia* var. *alba* Goodman, Rhodora 38: 239. 1936. TYPE: U.S.A. Oklahoma: Murray Co., Arbuckle Mts., 7 Apr. 1934, *George J. Goodman* 2077 (holotype, OKL).

Physaria pallida (Torrey & A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria grandiflora* Hooker var. *pallida* Torrey & A. Gray, Fl. N. Amer. 1: 101. 1838. *Lesquerella pallida* (Torrey & A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 253. 1888. TYPE: U.S.A. Texas: San Augustine Co., near St. Augustine, *Melinae C. Leavenworth s.n.* (holotype, NY).

Physaria palmeri (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella palmeri* S. Watson, Proc. Amer. Acad. Arts 23: 255. 1888. TYPE: Mexico. Baja California: Topo Cañon, Lower California, 1884, *C. R. Orcutt* 1099 (holotype, GH).

Physaria parviflora (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella parviflora* Rollins, J. Arnold Arbor. 64: 506. 1983. TYPE: U.S.A. Colorado: Rio Blanco Co., USGS Black Cabin Gulch Quadrangle, T3S, R100W, S13, 3/4 mi. S of spring in Tommy's Draw, 2595 m, 21 July 1982, *W. Baker & S. Sigstedt* 82-308 (holotype, GH; isotype, CS).

Physaria parvula (Greene) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella parvula* Greene, Pittonia 4: 308. 1901. TYPE: U.S.A. Colorado: Grand Co., summit of Mt. Bross, Middle Park, 29 July 1876, *H. N. Patterson s.n.* (holotype, NDG; isotypes, F, MO, NY, US).

Physaria paysonii (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella paysonii* Rollins, Contr. Gray Herb. 171. 44. 1950. TYPE: U.S.A. Wyoming: Lincoln Co., mountains near Cottonwood Lake, E of Smoot, 13 Aug. 1923, *Edwin B. Payson & George M. Armstrong* 3816 (holotype, GH; isotypes, COLO, MO).

Physaria pendula (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella pendula* Rollins, Cruciferae of Continental N. Amer. 647. 1993. TYPE: U.S.A. Nevada: White Pine Co., Snake Range, 3 km E of Murphy Wash road to Big Springs Wash, T10N, R68E, 6450 ft., 23 May 1985, *Arnold Tiehm* 9480 (holotype, GH).

- Physaria peninsularis*** (Wiggins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella peninsularis* Wiggins, Contr. Dudley Herb. 1: 166. 1933. TYPE: Mexico. Baja California: La Encantada, Sierra San Pedro Mártir, 18 Sep. 1930, *Ira L. Wiggins & L. Demaree 4919* (holotype, DS; isotypes, GH, UC, US).
- Physaria pinetorum*** (Wooton & Standley) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella pinetorum* Wooton & Standley, Contr. U.S. Natl. Herb. 16: 126. 1913. TYPE: U.S.A. New Mexico: Lincoln Co., Gilmores Ranch on Eagle Creek, White Mts., 2200 m, 25 Aug. 1907, *Elmer O. Wooton & Paul C. Standley 3460* (holotype, US; isotype, NMC).
- Physaria prostrata*** (A. Nelson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella prostrata* A. Nelson, Bull. Torrey Bot. Club 26: 124. 1899. TYPE: U.S.A. Wyoming: Uinta Co., Piedmont, 7 June 1898, *Aven Nelson 4564* (holotype, RM; isotypes, B, NY, US).
- Physaria pruinosa*** (Greene) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella pruinosa* Greene, Pittonia 4: 307. 1901. TYPE: U.S.A. Colorado: Archuleta Co., Pagosa Springs, 21 July 1899, *Charles F. Baker s.n.* (holotype, NDG).
- Physaria pueblensis*** (Payson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella pueblensis* Payson, Ann. Missouri Bot. Gard. 8: 169. 1922. TYPE: Mexico. Puebla: vicinity of San Luis Tultitlanapa, *Carl. A. Purpus 3389* (holotype, MO; isotypes, F, GH, NY, UC, US).
- Physaria pulchella*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella pulchella* Rollins, Novon 5: 72. 1995. TYPE: U.S.A. Montana: Beaverhead Co., S-facing slope along Trapper Creek just S of Hecha Mines, Pioneer Mts., T3S, R11W, Sec. 32, 8600 ft., 25 July 1991, *Peter Lesica 5525 & Steve Cooper* (holotype, GH; isotype, MONTU).
- Physaria purpurea*** (A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria purpurea* A. Gray, Smithsonian Contr. Knowl. (Pl. Wright.) 5: 14. 1853. *Lesquerella purpurea* (A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 253. 1888. TYPE: U.S.A. Texas: El Paso Co., near El Paso, *Wright 1320* (holotype, GH; isotypes, GH, MO).
- Physaria rectipes*** (Wooton & Standley) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella rectipes* Wooton & Standley, Contr. U.S. Natl. Herb. 16: 127. 1913. TYPE: U.S.A. New Mexico: without locality, 6 June 1883, *C. C. Marsh 81* (holotype, US).
- Physaria recurvata*** (Engelmann ex A. Gray) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria recurvata* Engelmann ex A. Gray, Bost. J. Nat. Hist. 6: 147. 1850. *Lesquerella recurvata* (Engelmann ex A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 253. 1888. TYPE: U.S.A. Texas: near Cibolo River, between San Antonio and New Braunfels, Mar. 1846, *F. Lindheimer 330* (lectotype, designated by Rollins & Shaw (1973), GH; isolectotype, MO).
- Physaria reediana*** O'Kane & Al-Shehbaz, nom. nov. Replaced name: *Vesicaria alpina* Nuttall ex Torrey & A. Gray, Fl. N. Amer. 1: 102. 1838. *Lesquerella alpina* (Nuttall ex Torrey & A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 251. 1888. TYPE: U.S.A. Wyoming: Natrona Co., Rocky Mt. range toward sources of the Platte, *Thomas Nuttall s.n.* (holotype, BM; isotypes, K, PH).
- This is named in honor of Reed C. Rollins (7 December 1911–28 April 1998) for his lifetime of contributions on the North American Brassicaceae, especially in the genera *Lesquerella* and *Physaria*. The transfer of *Vesicaria alpina* to *Physaria* would create a later homonym of *P. alpina* Rollins (Rollins, 1981).
- Physaria reediana* subsp. *spatulata*** (Rydberg) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella spatulata* Rydberg, Contr. U.S. Natl. Herb. 3: 486. 1896. TYPE: U.S.A. South Dakota: Lawrence Co., Deadwood, 1600 m, *Per A. Rydberg 534* (holotype, US; isotype, NY).
- Lesquerella spatulata* was reduced by Rollins and Shaw (1973) to synonymy of *L. alpina* and was treated by Rollins (1993) as a variety of the latter. It is maintained herein at the subspecific level in *Physaria*.
- Physaria rosei*** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella rosei* Rollins, Contr. Gray Herb. 214: 23. 1984. Based on *Synthlipsis lepidota* Rose, Contr. U.S. Natl. Herb. 8: 294. 1905, non *Physaria lepidota* Rollins, Brittonia 33: 335. 1981. TYPE: Mexico. Hidalgo: calcareous soil near Tula, 6800 ft., *Pringle 6899* (holotype, US; isotypes, B, GH, M, MO, NY, US).

- Physaria rosei** subsp. **perotensis** (Rollins) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella rosei* var. *perotensis* Rollins, Contr. Gray Herb. 214: 23. 1984. TYPE: Mexico. Veracruz: Bosque de Pinos, alrededores de Perote, 2700 m, 21 Apr. 1976, *Sergio Aven- daño R. et al.* 201 (holotype, GH).
- Physaria schaffneri** (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Vesicaria schaffneri* S. Watson, Proc. Amer. Acad. Arts 17: 320. 1882. *Lesquerella schaffneri* (S. Watson) S. Watson, Proc. Amer. Acad. Arts 23: 254. 1888. TYPE: Mexico. San Luis Potosí: San Luis Potosí, *J. G. Schaffner* 150 (holotype, GH; isotype, F).
- Physaria sessilis** (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella gracilis* (Hooker) S. Watson var. *sessilis* S. Watson, Proc. Amer. Acad. Arts 23: 253. 1888. *Lesquerella sessilis* (S. Watson) Small, Fl. SE U.S. 471. 1903. TYPE: U.S.A. Texas: Uvalde Co., Rio Frio and Leona, May 1851, *Wright* 848 (lectotype, designated by Rollins & Shaw (1973), GH; ?isolectotypes, GH, NY).
- Physaria sinuosa** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella sinuosa* Rollins, Contr. Gray Herb. 214: 23. 1984. TYPE: Mexico. Puebla: N of Tehuacan, 5650 ft., 19 Nov. 1966, *Harry D. Ripley* & *Rupert C. Barneby* 14734 (holotype, GH; isotype, NY).
- Physaria subumbellata** (Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella subumbellata* Rollins, Amer. J. Bot. 26: 420. 1939. TYPE: U.S.A. Utah: Uintah Co., foothills of Uinta Mts., 18 mi. N of Vernal, 17 June 1937, *Reed C. Rollins* 1758 (holotype, GH).
- Physaria tenella** (A. Nelson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella tenella* A. Nelson, Bot. Gaz. 47: 426. 1909. TYPE: U.S.A. Nevada: Clark Co., Moapa, 8 Apr. 1905, *Leslie N. Goodding* 2184 (holotype, RM; isotypes, GH, MO, UC).
- Physaria thamnophila** (Rollins & E. Shaw) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella thamnophila* Rollins & E. Shaw, Genus *Lesquerella* in N. Amer. 86. 1973. TYPE: U.S.A. Texas: Zapata Co., 3 mi. SE of Zapata, near US Hwy. 83, *Reed C. Rollins* & *Donovan S. Correll* 5949 (holotype, GH; isotype, LL).
- Physaria tumulosa** (Barneby) O'Kane & Al-Shehbaz, comb. et stat. nov. Basionym: *Lesquerella hitchcockii* Munz subsp. *tumulosa* Barneby, Leaflet West. Bot. 10. 313. 1966. TYPE: U.S.A. Utah: Kane Co., 6.5 mi. SE of Cannonville, just S of the Garfield County line, 5700 ft., 12 June 1966, *Rupert C. Barneby* 14424 (holotype, NY; isotypes, BRY, CAS, GH, UC, US, UTC).
- Reveal (1970) raised *Lesquerella hitchcockii* subsp. *tumulosa* to specific rank, but Rollins (1993) reduced it to synonymy of *L. rubicundula*. Because of its pulvinate habit and filiform-linear leaves 0.7–1 mm wide, we agree with Reveal in recognizing subspecies *tumulosa* as a distinct species. The remainder of the *Physaria hitchcockii* complex (except *L. navoensis*) are more loosely caespitose and with leaves distinctly wider than those of *P. tumulosa*.
- Physaria utahensis** (Rydberg) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella utahensis* Rydberg, Bull. Torrey Bot. Club 30. 252. 1903. TYPE: U.S.A. Utah: Utah Co., American Fork Canyon, 31 July 1880, *Marcus E. Jones* 1354 (holotype, NY; isotypes, ARIZ, DS, MO, US).
- Physaria valida** (Greene) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella valida* Greene, Pittonia 4: 68. 1899. TYPE: U.S.A. New Mexico: Gray, 1898, *Josephine Skehan s.n.* (holotype, NDG; isotypes, NY, US).
- Physaria vicina** (Anderson, Reveal & Rollins) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella vicina* Anderson, Reveal & Rollins, Novon 7: 9. 1997. TYPE: U.S.A. Colorado: Montrose Co., small flat-topped mesa overlooking Uncompahgre River just S of 66500 Kinikin Road, ca. 4 air mi. SE of Montrose, 6050 ft., sec. 10, T48N, R9W, 29 June 1995, *James L. Reveal* 7492 (holotype, GH; isotypes, BM, BRY, COLO, MARY, MO, NY, RM, TEX, US, US).
- Physaria wardii** (S. Watson) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella wardii* S. Watson, Proc. Amer. Acad. Arts 23: 255. 1888. TYPE: U.S.A. Utah (as Arizona): Garfield Co., Aquarius Plateau, 11,000 ft., 16 Aug. 1875, *L. F. Ward* 589 (holotype, GH; isotypes, F, MO, US).
- Lesquerella kaibabensis* Rollins, Contr. Gray Herb. 211: 110. 1982. Syn. nov. TYPE: U.S.A. Arizona: Coco-

nino Co., Grand Canyon National park, 18.6 mi. S of Jacob Lake on road to N entrance of the park, 8 June 1979, *Reed C. & Kathryn W. Rollins 79191* (holotype, GH; isotype, MO).

A critical examination of the type collections of *Lesquerella wardii* and *L. kaibabensis* reveals that they are indistinguishable in every morphological aspect. The alleged differences in flower color and style length (Rollins, 1993) do not hold. On the Kaibab Plateau of northern Arizona, populations of *L. wardii* vary from all white flowered, to all yellow flowered, to mixed white and yellow.

Physaria wyndii (Rollins & E. Shaw) O'Kane & Al-Shehbaz, comb. nov. Basionym: *Lesquerella wyndii* Rollins & E. Shaw, Genus *Lesquerella* in N. Amer. 154. 1973. TYPE: Mexico. Coahuila: Sierra del Carmen, Cañon de Sentenela on Hacienda Piedra Blanca, Wynd & Mueller 517 (holotype, GH; isotypes, ARIZ, MEXU, MO, NY, OKLA, US).

EXCLUDED SPECIES

The following taxa are excluded from *Lesquerella* and now placed in the new genus *Paysonia* (see O'Kane & Al-Shehbaz in this issue of *Novon*).

Lesquerella auriculata (Engelmann & A. Gray) S. Watson, Proc. Amer. Acad. Arts. 23: 250. 1888.
Lesquerella densipila Rollins, Rhodora 54: 186. 1952.
Lesquerella grandiflora (Hooker) S. Watson, Proc. Amer. Acad. Arts 23: 250. 1888.
Lesquerella lasiocarpa (Hooker ex A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 251. 1888.
Lesquerella lasiocarpa var. *berlandieri* (A. Gray) Payson, Ann. Missouri Bot. Gard. 8: 139. 1922.
Lesquerella lasiocarpa var. *heterochroma* (S. Watson) Rollins, Rhodora 57: 245. 1955.
Lesquerella lescurii (A. Gray) S. Watson, Proc. Amer. Acad. Arts 23: 250. 1888.
Lesquerella lyrata Rollins, Rhodora 57: 252. 1955.
Lesquerella perforata Rollins, Rhodora 54: 190. 1952.
Lesquerella stonensis Rollins, Rhodora 57: 255. 1955.

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